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THE TAXONOMY OF THE BRITISH SPECIES OF *ENTOMOBRYA* (COLLEMBOLA)

By A. South

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With 58 Text-figures

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I. Introduction

Entomobrya was first recognised as a separate genus by Nicolet in 1841, when he created the genus under the name of *Degeeria*. In 1848 Gistel renamed the genus *Mydonius*, as *Degeeria* was preoccupied by a genus of Diptera. This was generally unknown and Rondani, upon discovering the synonomy of *Degeeria* in 1861, renamed the genus *Entomobrya*. Two other workers, Laing and Salmon, rediscovered the name *Mydonius* independently in 1945, but the name *Entomobrya* was validated under Plenary Powers by the International Commission for Zoological Nomenclature in 1957.

Lubbock (1873) revised the European members of the genus and considered that there were sixteen species and six synonyms. A world revision by Brook (1884) reduced the world list from twenty-four species with eight synonyms to eleven species

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with twenty-one synonyms. Bonet (1934) published a key to more than one hundred world species and also listed twenty-seven that he was unable to recognise.

Gisin (1947) discussed the specific status of three Swiss members of what he called the *E. nivalis* group. Christiansen (1958*a*) revised the Nearctic members of the genus, in the light of new morphological characters considered by him to be significant. These characters are discussed below in section III.

Considerable confusion exists in the literature on *Entomobrya*, owing to the lack of good taxonomic characters. The colour pattern has been used as the basis of most keys to the genus and some confusion has resulted, since in most species the colour pattern varies widely within a population. The pattern variation was found, in the course of the present work, to fall into clearly defined limits for each species. Colour pattern has therefore been used to distinguish the different species and the conclusions reached have been supported by some biological experiments.

Gisin (1960) listed twenty-two European species of *Entomobrya* s. str. Of these, seven have been recorded only from Eastern Europe and, of the remaining fifteen species, ten have been recorded from the British Isles. Since Gisin included *E. intermedia* Brook as a synonym of *E. muscorum* (Nicolet) and *E. maritima* Reuter as a synonym of *E. lanuginosa* (Nicolet), and listed *E. macrocerata* Bagnall as a *species dubia*, the total number of recorded British species of *Entomobrya* stands at thirteen.

The species are :—

E. albocincta (Templeton, 1835)
E. arborea (Tullberg, 1871)
E. corticalis (Nicolet, 1841)
E. intermedia Brook, 1884
E. macrocerata Bagnall, 1917
E. marginata (Tullberg, 1871)
E. maritima Reuter, 1891
E. multifasciata (Tullberg, 1871)
E. muscorum (Nicolet, 1841, *nec* Tullberg, 1871)
E. nicoleti (Lubbock, 1868)
E. nivalis (Linnaeus, 1758)
E. pulchella (Ridley, 1881)
E. superba (Reuter, 1876)

The British status of *E. superba* is doubtful. The only record is the inclusion of the species in the key to the Collembola of Ireland by Womersley (1930) and in this work no other data are given ; the species may therefore have been included in the key as a possible British species and for no other reason. Kloet and Hincks (1945) record a *Mydonius arboreus* from Britain. The only other record of this species is the description of an *E. multifasciata* var. *arborea* by Parfitt (1891) from Devon, and there is no evidence that this form is synonymous with *E. arborea* (Tullberg). *E. macrocerata* is described as a synonym of *E. intermedia* by the present author in a paper in preparation.

E. marginata has been recorded on nine occasions from Britain. It was not possible to check these records, as in each instance they occur in lists of Collembola with no other data. Three specimens of *E. marginata* examined in the British Museum (Nat. Hist.) collection and identified by the same worker in 1926 and 1938 proved to be *E. multifasciata*, *E. nicoleti* and *E. nivalis*. There is considerable confusion in the literature with regard to the identification of *E. marginata*. Brook (1884) describes it as a synonym of *E. multifasciata*, and it seems probable that the British status of the species is doubtful.

The present author considers that the above four species, *E. superba*, *E. arborea*, *E. macrocerata* and *E. marginata*, are not members of the British fauna for the reasons given and that the British list of *Entomobrya* consists of the nine remaining species from the above list.

II. Methods

Cultures of each species were maintained in the laboratory in small glass heat-resisting dishes, 3·5 cm. deep and 5 cm. wide. The dishes were sterilised in an oven before use and fitted with corks covered with a layer of thin polythene sheeting which had been previously sterilised in 70 per cent. alcohol. The bottom of the dish was covered with white filter paper, moistened with sterile distilled water, and 20–30 insects were kept in each dish. The food used was the fungus *Cladosporium herbarum*, cultured on potato agar, the agar being cut into 2 cm. squares which were placed on the filter paper in the dishes. It was found that *Entomobrya* could be successfully anaesthetised with carbon dioxide gas, provided that the specimens were sorted on damp filter paper. This method was especially useful when making up cultures from samples taken in the field.

Samples were fixed in Gisin's fixative, and stored in 90 per cent. alcohol. Specimens for detailed examination were then mounted in polyvinyl lactophenol using thin slides (0·8 /1·0 mm.) and No. 0 cover glasses. Some morphological characters were more readily seen if the specimens were bleached in diaphanol and then stained in chlorazol black before mounting. Some specimens were mounted in *n*-butyl methacrylate polymer blocks by a modification of the embedding process described by Challice (1954). This enabled the lateral colour pattern to be seen without distortion.

III. The Genus *Entomobrya*

(1) *Diagnosis of the Family Entomobryidae*

Body scaled or covered with thickly ciliated clubbed setae; abdomen III and IV clearly differing in length; abdominal segments never fused; furca well developed; trochanteral organ well developed; postantennal organ lacking.

(2) *Diagnosis of the Genus* Entomobrya

Unscaled; antenna 4-segmented; abdomen IV much longer than abdomen III; eyes 8 + 8; mucro bare with basal spine and ante-apical tooth.

(3) *Discussion of Taxonomic Characters*

The following characters have been used by various authors to distinguish between the species of *Entomobrya*:

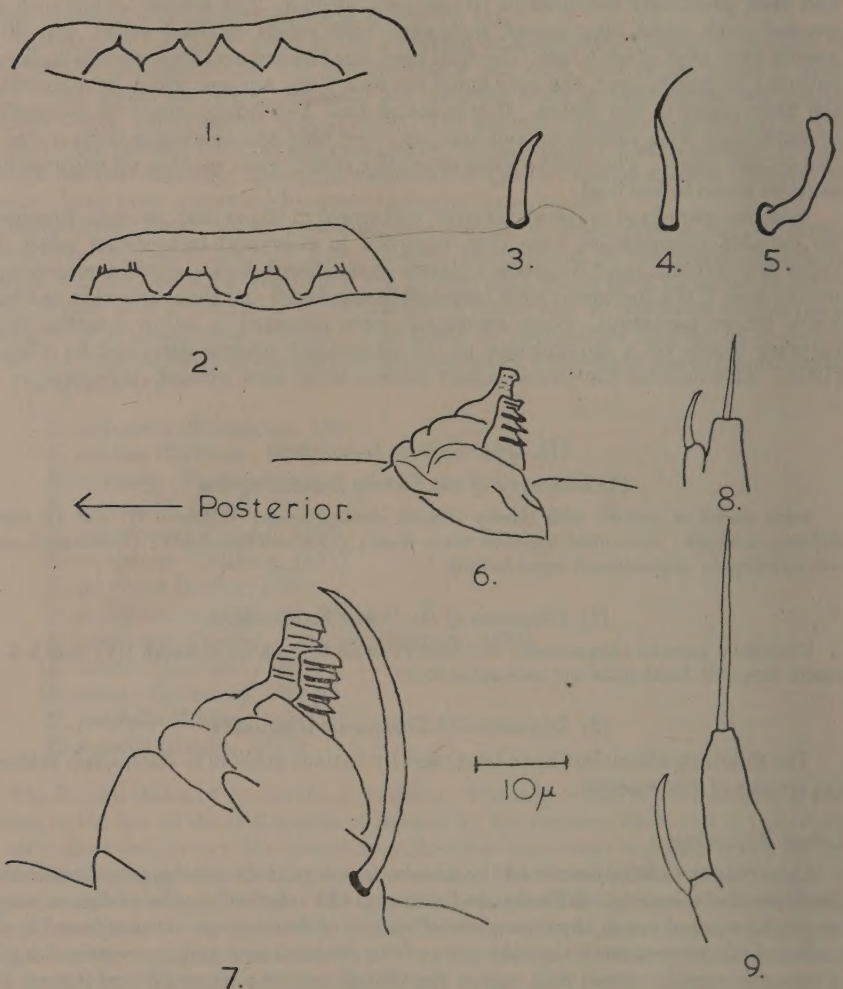
Labial Appendage

Christiansen (1958*a*) described the labial appendage in *Entomobrya* and stated that the form of the external differentiated seta and the relative lengths of this seta and its papilla were of use in the separation of species of *Entomobrya*. It was found in the course of the present work that the form of the external seta and the relative lengths of seta and papilla varied with age in the British species; figures 8 and 9 show the relative lengths of external seta and papilla in the first and sixth instars of *E. multifasciata*, respectively, and this condition is typical of all the species examined. The seta extends for some distance beyond the tip of the papilla in the first instars, and the relative length of the papilla gradually increases in succeeding instars until the seta is shorter than the papilla in the mature instars. The shape of the seta also varies and is frequently rather curved in the younger instars and straight in the mature insect. This character is therefore of little use for British *Entomobrya*.

Labrum

The labral papillae were shown by Christiansen (*loc. cit.*) to be specific in some instances. The form of the papillae in all the species examined, with one exception, was broadly truncate with several small setae rising from the surface of the papilla.

This form is similar to that described by Christiansen for *E. nivalis*. The labral papillae of *E. corticalis* are unisetaceous and tapered as in figure 1, and resemble those described by Christiansen for *E. unostrigata* Stach, *E. triangularis* Schott and several other species. The form of the papilla of the other British species is illustrated in figure 2.



FIGS. 1–9.—(1) Labral papillae of *Entomobrya corticalis*; (2) the same, *E. multifasciata*. (3) Seta of male genital plate of *E. corticalis*; (4) the same, *E. intermedia*. (5–9) *E. multifasciata*: (5) Basal seta of male genital plate; (6) lateral aspect of retinaculum, first instar; (7) the same, sixth instar; (8) external differentiated seta and papilla of first instar; (9) the same, sixth instar.

Unguis and Empodial Appendage

A number of authors have described differences in the form and number of the teeth on the unguis. Most of these differences have been due to the difficulties involved in examining such a small structure, and no real differences were observed during the present work; the teeth of the unguis of *E. pulchella* appeared to be more exaggerated than in the other species but this may be only an age difference, since only mature

specimens of this species were examined. In several specimens of *E. multifasciata* the unguis was seen to be split into two similar halves.

Handschin (1929) and Christiansen (1958*a*) have observed a fine ciliation on the posterior edge of the lamellae on the empodial appendage in some species of *Entomobrya* and one British species, *E. pulchella*, possesses this ciliation. Handschin (*loc. cit.*) illustrated the empodial appendage of this species in his work on German Collembola.

Trochanteral Organ

Christiansen (1958*a*) stated that this organ was of some taxonomic value. He considered that the number of internal setae was of use in supporting the identification of species, and also compared the lengths of the arms in different species. It has been shown in the present work that the organ varies considerably in each species and with age, and that the number of internal setae and the arrangement of these is very variable. This character is therefore of little specific use, although of considerable importance in determining the instar of specimens.

Male Genital Plate

The genital plate of *Entomobrya* was described by Christiansen (1958*c*) as papillate. He also stated (1958*a*) that the form of the 12 to 14 setae round the outer margin of the papilla was very specific. The basal pair of setae in the British species examined were similar in each species and were flattened, wide, a little expanded apically and in most instances truncate (fig. 5). The other setae showed a common form in all but one species (fig. 4), and were slender, suddenly constricted about half-way along their length and filamentous beyond this point. They reached or extended beyond the central papilla of the plate. In *E. corticalis*, these setae are short and blunt and do not reach the central papilla (fig. 3).

Colour Pattern

The general body colour of *Entomobrya* varies and is probably dependent in part on the food eaten, as has been demonstrated for *Onychiurus* by Choudhuri (1958). The colours recorded for *Entomobrya* vary between white and yellow through to light green and brown. Male specimens of *E. multifasciata* reared in the laboratory are rather darker than female specimens.

The pattern pigment is situated in the dermis and varies between purple and black. In the present work specimens have been examined, particularly of *E. multifasciata* and *E. nivalis*, from several countries other than Britain, and the range of pattern variation has been recorded. It was found that the pattern of each species varied between definite limits and these are described below. The full pattern appears towards the end of the first instar and the only subsequent changes observed were in the intensification of the pattern already present. It was observed also that specimens reared at low temperatures were pale and those reared at high temperatures (24° C. and above) were more darkly pigmented (fig. 31). It was observed on numerous occasions that a series of specimens of a species from one habitat showed a wide range of pattern variation.

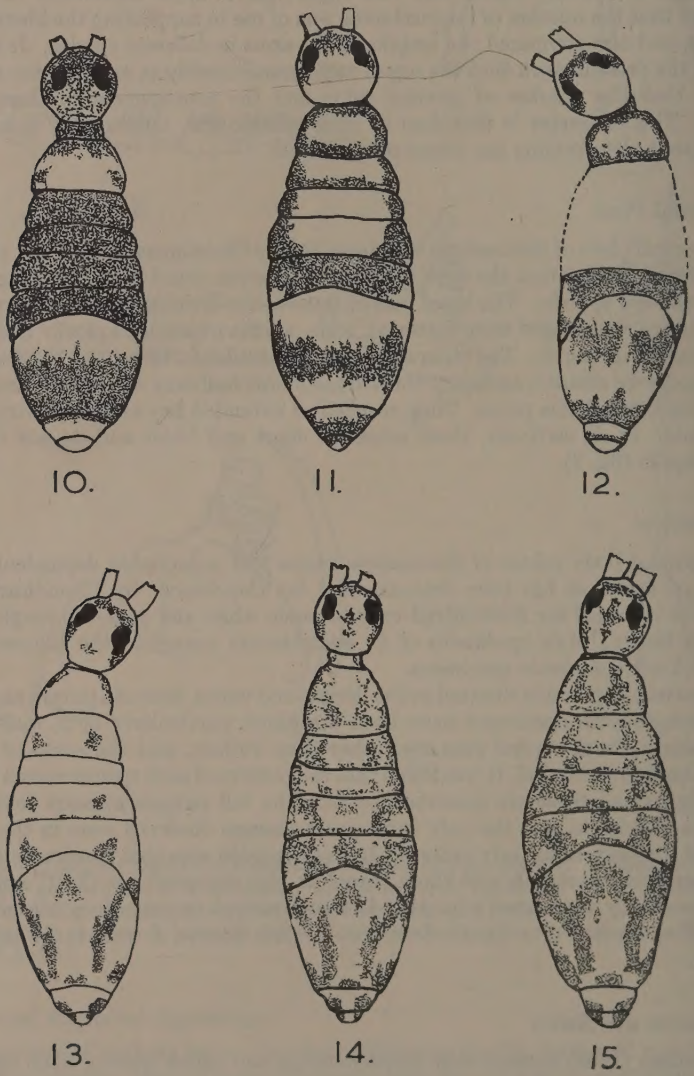
Measurements and Ratios

Christiansen (1954) showed that measurements and ratios were of little use in the study of *Entomobrya*. Measurements made during the present work confirm this conclusion, one reason for this variation in measurements being the stretching of the intersegmental membranes when the insect is mounted.

Other Characters

Other taxonomic characters used by some authors include the form of the mucronal teeth, the body setae, antennal sense organs and the retractile bulb at the apex of the fourth antennal segment. No difference in these characters was observed in the British species of *Entomobrya*.

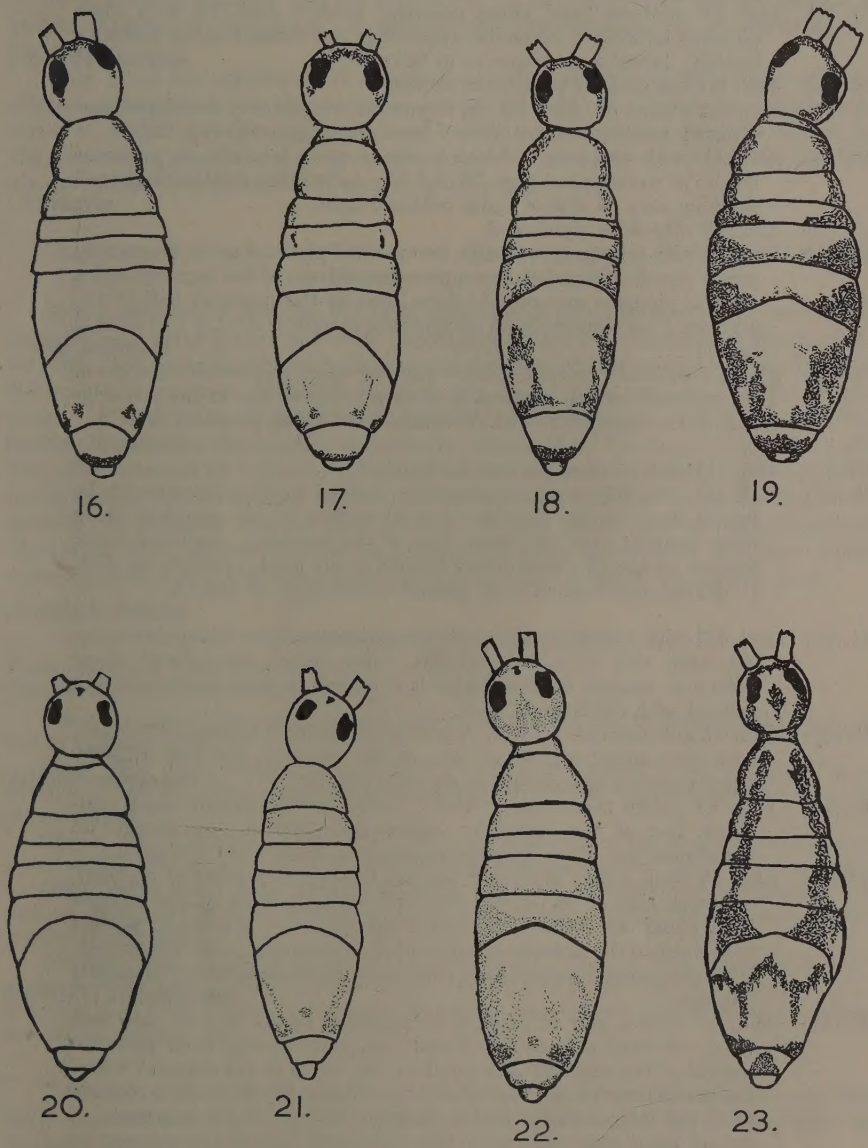
Christiansen's characters (1958*a*) appear to have little significance in the systematics of British *Entomobrya*. The use of the male genital plate is limited, as the number of male specimens taken in samples is small and the plate is only visible if the insect is mounted with the furca contracted. The use of the plate is also suspect since



FIGS. 10–15.—Diagrams of pattern distribution in the British species of *Entomobrya*: (10) *E. albocincta*; (11) *E. corticalis*; (12) *E. pulchella* (incomplete, specimen damaged); (13–15) *E. intermedia*.

Christiansen (1958*c*) showed that there is considerable variation in the form of the setae of the plate in *Entomobryoides guthriei* (Mills) in different geographical races.

The morphological characters are of limited practical application, and the key of Christiansen (1958*a*) to the Nearctic *Entomobrya* is based on characters that apply to only a few of the specimens taken in any samples, *e.g.* the use of the genital plate described above. He also resorts to the use of colour pattern in several instances.



FIGS. 16–23.—Diagrams of pattern distribution in the British species of *Entomobrya*: (16–19) *E. nicoleti*; (20–22) *E. maritima*; (23) *E. muscorum*.

IV. Key to the British *Entomobrya*

1 (6) Abd. III entirely pigmented dorsally.

2 (3) Th. III, Abd. I, II, and III all entirely pigmented dorsally **albocincta** (Templeton)

3 (2) No segment other than Abd. III entirely pigmented dorsally.

4 (5) Abd. IV with band along posterior border. Abd. VI unpigmented; empodial appendage ciliated along posterior border; labral appendages as in figure 2 . . . . . **pulchella** (Ridley)

5 (4) Abd. IV without band along posterior border, Abd. VI with some pigment laterally; empodial appendage not ciliated along posterior border; labral appendages as in figure 1 . . . **corticalis** (Nicolet)

6 (1) Abd. III not entirely pigmented dorsally.

7 (12) Pigment absent on Abd. III or, if present, very poorly developed and diffuse; posterior dorsal part of head also pigmented (fig. 22).

8 (9) Abd. IV with one pair of black pigment spots laterally on posterior border of the segment (figs. 32 and 33); a pale but distinct V-shaped marking may be visible under reflected light . . . . . **nivalis** (L.)

9 (8) Abd. IV otherwise pigmented.

10 (11) Abd. IV with no pigment or with two pairs of pigment spots, frequently partly fused, lying laterally on posterior margin of the segment and a distinct pigment spot on mid-dorsal line in the posterior half of the segment; no pigment band on posterior margin of Abd. V (*see* Note 2, below) . . . . . **maritima** Reuter

11 (10) Abd. IV with two pairs of distinct pigment spots on posterior margin of the segment but no pigment spot on mid-dorsal line in the posterior half of the segment; Abd. V with a band along posterior margin **nicoleti** (Lubbock)

12 (7) Abd. III with distinct pattern markings.

13 (14) Abd. III with diffuse pigment dorsally, formed by the extension of the lateral bands on to the dorso-lateral surface of the segment which never reaches the mid-dorsal line of the segment; pigment never present on the posterior dorsal surface of the head; pattern on Abd. IV diffuse, but distinct from ground colour (figs. 18 and 19) **nicoleti** (Lubbock)

14 (13) Abd. III with a well-marked pattern consisting of two triangular spots, one each side of mid-dorsal line, often joined by a band along posterior margin of the segment; dorsal pattern never entirely merged with the lateral bands.

15 (16) Abd. VI not pigmented; Abd. V with a well marked triangular pigment spot lying along mid-dorsal line of the segment, the base running along posterior margin of the segment (fig. 23) . . . **muscorum** (Nicolet)

16 (15) Abd. VI partly pigmented; Abd. V rarely with pigment along mid-dorsal line of the segment; where the pigment does extend to mid-dorsal line, then the pigment on Abd. VI is well developed.

17 (18) Abd. IV with a pair of clearly marked triangular patches of pigment, one each side of mid-dorsal line and with the base of the triangle lying along the posterior margin of the segment; where the patches are joined to the anterior cross band of the segment, then the connectives are poorly developed and run only from the apex of the triangular patches . . . . . **multifasciata** (Tullberg)

18 (17) Abd. IV with a pair of parallel, longitudinal bands of even thickness lying one each side of mid-dorsal line, and running from posterior margin of the segment to a point in the centre of the segment where the bands terminate and a branch runs diagonally forward to connect with the lateral bands in the anterior margin of the segment; a second band may run across the mid-dorsal line of the segment to connect with its opposite number.

19 (20) Abd. IV without inner cross band running over mid-dorsal line between the pair of parallel bands, or if this band is present it runs directly

between the longitudinal bands and never into the anterior half of the segment . . . . . **nivalis** (L)

20 (19) Abd. IV always with an inverted V-shaped mark in mid-dorsal line of the segment, the apex of this mark lying near the anterior border of the segment ; the pair of longitudinal bands may be joined through this band but are never joined by a band running directly over the mid-dorsal line of the segment . . . . . **intermedia** Brook

Note 1.—The pigment pattern referred to in the key is the pattern formed of purple or purple-black pigment; no reference has been made to the ground or general body colour.

Note 2.—A few specimens of *E. maritima* have been taken with traces of faint diffuse pigmentation on the posterior border of Abd. V. These specimens were, however, rather strongly pigmented and could be distinguished from *E. nicoleti* by the presence of pigment on the posterior dorsal surface of the head (fig. 22), which is absent in heavily pigmented *E. nicoleti* specimens (fig. 19).

V. Diagnosis of the British Species of *Entomobrya*, with Notes on Synonymy and Distribution of Each Species

It was possible to examine the type specimen of only one species, *E. intermedia*, during the course of the present work. Several topotypes of *E. muscorum* were examined and found to agree closely with the original diagram of this species by Nicolet. The following species were identified without any doubt from original descriptions and plates : *E. albocincta*, *E. corticalis*, *E. maritima*, *E. multifasciata* and *E. nicoleti*. The darker forms of the last species were clearly illustrated by Tullberg (1872). *E. nivalis* was not illustrated by Linnaeus (1758) but several authors, including Tullberg (1872), included illustrations in their work and these leave no doubt as to the identity of the species. *E. pulchella* was not illustrated by Ridley (1881) but subsequent authors illustrated this species without any disagreement, Handschin's diagram (1929) agreeing closely with the specimens examined in the course of the present work.

Entomobrya albocincta (Templeton)

Podura albocincta Templeton, 1835, *Trans. ent. Soc. Lond.* **1** : 95.
Degeeria cincta Lubbock, 1862, *Trans. Linn. Soc. Lond.* **23** : 594.

Antennae : Ant. I pale with thin purple-black ring at apex, Ant. II purple distally, Ant. III and IV entirely purple.

Head : eyes black, connected anteriorly by a purple-black band ; anterior half of head dorsally covered by diffuse purple pigment, ventrally with broad median longitudinal band of diffuse purple.

Thorax : Th. II dorsally and anteriorly with a broad transverse purple band, remainder of dorsal surface of head pale, with two lateral purple patches posteriorly ; Th. III dorsally purple.

Legs : precoxae and coxae proximally tinged with purple in prothoracic and mesothoracic legs, remainder of legs pale ; metathoracic legs, with exception of tibiotarsus, purple ; femur frequently pale distally.

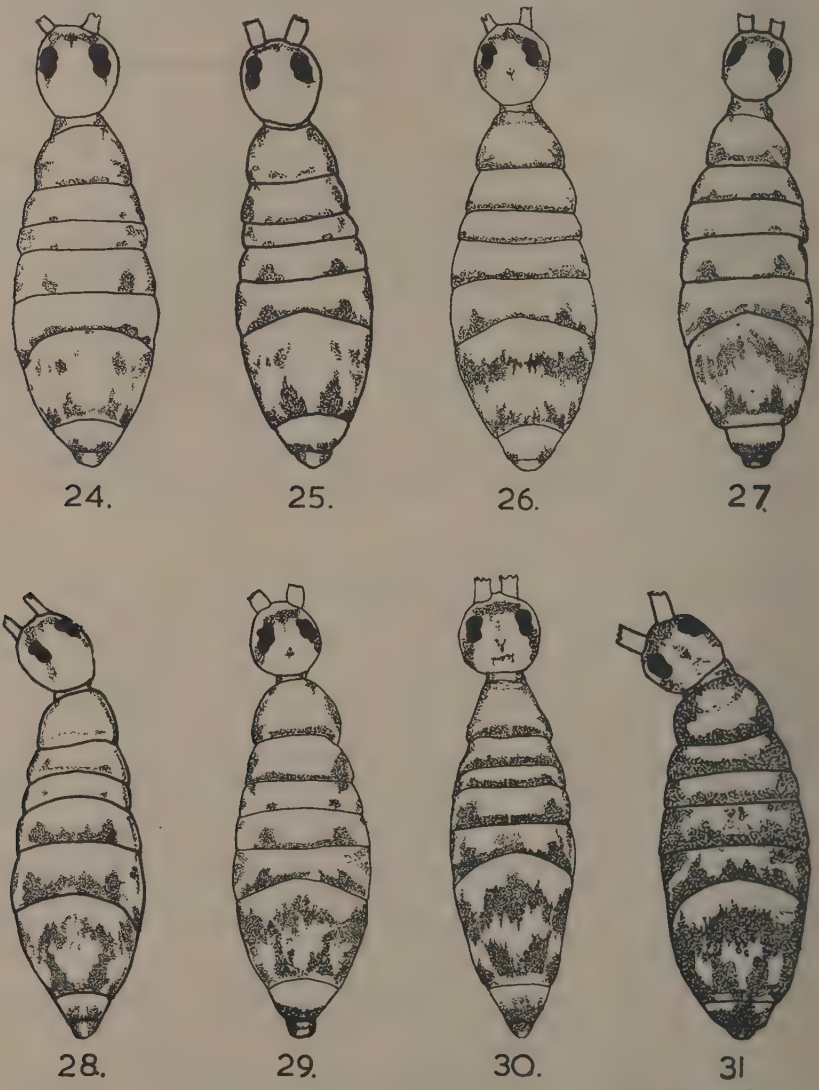
Abdomen : Abd. I, II and III dorsally entirely purple ; Abd. IV with broad purple band across posterior half of segment, Abd. V with thin band of purple along the anterior border, otherwise Abd. V and VI pale ; manubrium usually with traces of pale purple pigment ; abdomen and thorax ventrally pale.

Variation.—The colour pattern of *E. albocincta* (fig. 10) is very constant, and the only observed variation was in the extent of the pigment over the dorsal surface of the head and anterior half of Abd. IV.

Material examined.—Ninety-four samples of *E. albocincta* from 15 counties in England and Wales were examined during the present work.

Geographical distribution.—E. albocincta has been recorded from 44 counties in the British Isles during the course of the present work and in the literature, and from the following countries :—Czechoslovakia (Uzel, 1891) ; Germany (Börner, 1901) ; France (Handschin, 1929) ; Sweden (Agrell, 1934, 1943) and Portugal (Da Gama, 1959).

Observations on the habitat.—E. albocincta is a corticole species ; the majority of the samples taken were from under loose dead bark of deciduous and coniferous trees, and the species appeared to be most common on the first seven or eight feet of the trunk. Specimens were taken from thirty species of tree and shrub, and were most frequent on tree trunks with a large area of loose bark. *E. albocincta* also occurred in small numbers in the moss and litter at the base of tree trunks.



Figs. 24–31.—Diagrams of pattern distribution in *Entomobrya multifasciata.*

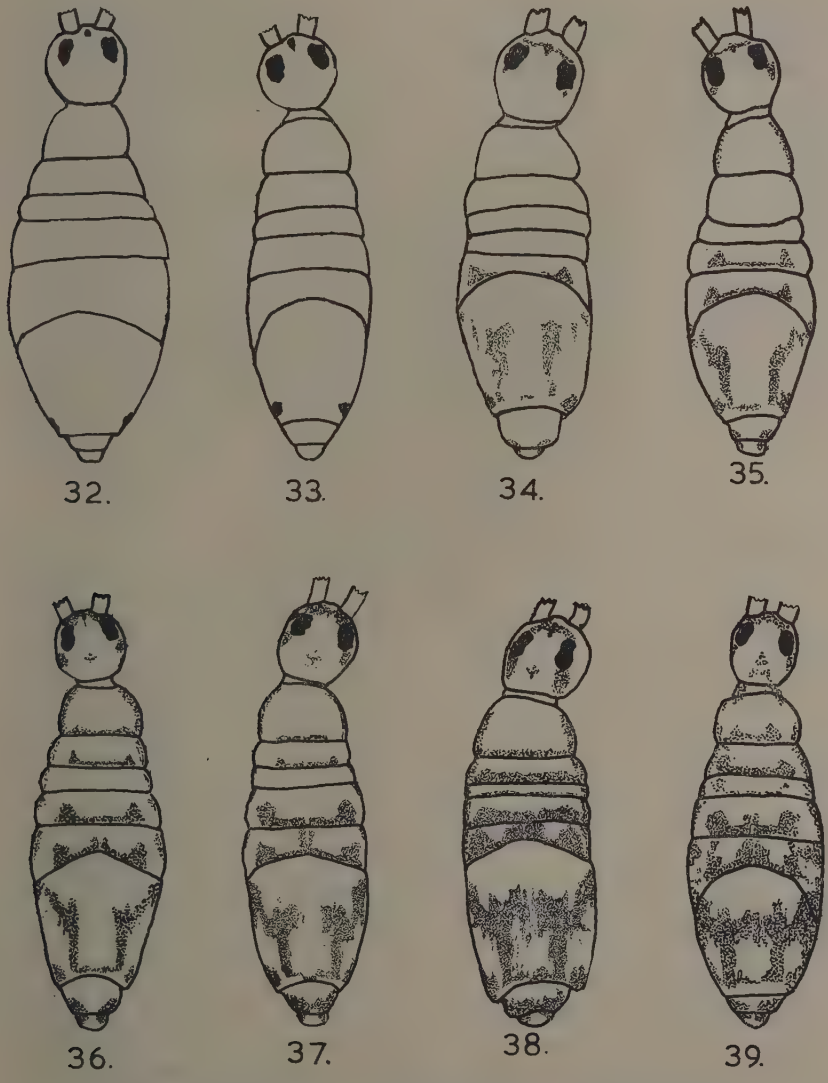
Entomobrya corticalis (Nicolet)

Degeeria corticalis Nicolet, 1841, *N. Denkschr. schweiz. Ges. Naturw.* **6** : 70.
Entomobrya multifasciata Brook, 1884, *J. Linn. Soc.* (*Zool.*) **17** : 275, *in partem.*

Antennae : as in *E. albocincta.*

Head : eye patches black, connected by a broad band of purple pigment, extending to sides of head ; remainder of head pale with an H-shaped marking on ventral posterior surface.

Thorax : Th. II dorsally with a thin purple band running transversely across anterior and posterior margins of segment ; laterally with a broad band of purple pigment from anterior margin of Th. II to posterior margin of Abd. III ; Th. III with a transverse band of purple across posterior margin of segment.



Figs. 32–39.—Diagrams of pattern distribution in *Entomobrya nivalis.*

Legs : pale with a variable band of pigment at distal end of femur of meso- and metathoracic legs and occasionally on prothoracic legs; tibiotarsus of metathoracic legs frequently with a diffuse purple band round middle of segment.

Abdomen : Abd. I and II with only lateral band referred to above, extending on to posterior dorsal region of Abd. III ; Abd. III entirely purple dorsally with the exception of 2 small pale patches laterally at posterior margin of segment where the lateral bands terminate ; Abd. IV with a broad transverse band across middle of segment, band becoming broader laterally ; Abd. V with a broad posterior purple band and Abd. VI with a broad anterior band which is continuous with the band on Abd. V ; abdomen and thorax ventrally pale ; manubrium pale.

Other characters : labral papillae unisetaceous (fig. 1) ; setae of male genital plate, other than basal setae, short and blunt, not extending beyond centre of plate (fig. 3).

Variation.—This species resembles *E. albocincta* in the absence of variation in the distribution of the colour pattern (fig. 11). The band on Abd. IV was never observed broken in the centre.

Material examined.—Forty-five samples of *E. corticalis* from one county in England were examined during the present work. Material was also examined from Switzerland and Germany, one sample in each instance.

Geographical distribution.—The samples of *E. corticalis* taken during the present work were from one locality (Sunninghill, Berkshire) and represent the first British record of this species. It has also been recorded from the following countries :— Austria (Torne, 1958) ; Finland (Linnaniemi, 1912) ; Germany (Schäffer, 1896) (Börner, 1901) ; Hungary (Stach, 1922) ; Poland (Schubert, 1933) ; Sweden (Ågren, 1903) ; Switzerland (Gisin, *in litt.*).

Observations on the habitat.—The specimens taken in the present work were found on the bark of *Acer pseudoplatanus* L. and *Crataegus monogyna* Jacq., and occurred in small isolated colonies of between 20–40 individuals, under the more firmly attached pieces of bark. It was rarely observed running on the surface of the bark. No specimens were found in litter taken from the base of the trees.

Entomobrya intermedia Brook

Entomobrya intermedia Brook, 1884, *J. Linn. Soc.* (*Zool.*) **17** : 274.
E. macrocerata Bagnall, 1916, *Lancs. Chesh. Nat.* **9** : 110.
E. nivalis Christiansen, 1958, *Bull. Mus. Comp. Zool. Harv.* **118** : 274.

Antennae : all segments pale purple. Ant. IV occasionally dark purple.

Head : eye patches black, joined anteriorly by a purple band which is also extended back dorsolaterally across the head on each side ; anchor-shaped marking present in most specimens on dorsal side of head near posterior margin.

Thorax : a pair of lateral bands running from anterior margin of Th. II to posterior margin of Abd. IV. Th. II and III, with a pair of irregular pigment patches one each side of mid-dorsal line, these patches extending forward in darker specimens and nearly reaching anterior margin of segment ; patches often joined by a narrow band of purple-black pigment running along posterior margin of segment.

Legs : tibiotarsus of all legs pale purple, also femur of metathoracic leg ; femur of meso- and metathoracic legs with a band of purple-black at apex.

Abdomen : Abd. I, II and III with similar markings to those of Th. II and III, in addition a patch of pigment situated anteriorly on mid-dorsal line of Abd. II and III, frequently extending back to posterior band of segment ; Abd. IV with a pair of posterior lateral patches confluent with the lateral longitudinal pigment bands ; short transverse band of pigment situated on posterior margin of segment across mid-dorsal line ; between lateral limits of this line and lateral patches a pair of longitudinal parallel bands of even thickness arise, just anterior to posterior margin of segment, running towards anterior margin of segment, forking about half way along segment into 2 branches of equal thickness, one branch running obliquely forward to join lateral band at anterior margin of segment and the other running to mid-dorsal line of segment where it joins its opposite number at a point just posterior to anterior border of Abd. IV ; the 2 inner branches form a characteristic inverted V-shaped marking on anterior half of segment ; Abd. V and VI with a pair of lateral spots on each segment.

Variation.—The limits observed during the course of the present work fall between the limits illustrated in figures 13–15. Most of the variation is due to intensification or reduction of the distribution of the pigment, no specimens having been observed with more pattern reduction than that shown in figure 13. The inverted V-shaped marking on the anterior of Abd. IV frequently fails to reach the parallel bands where they fork (figs. 13 and 14) but the pigment reduction always moves from the fork of the bands towards the apex of the V and all the specimens examined showed the apex of the V at least. This mark is therefore characteristic of the species. The thin transverse bands of Th. II to Abd. III are often reduced or missing and the series of pigment patches on the dorsal surface of the segments gives the appearance of a pair of longitudinal bands running along these segments. In heavily pigmented forms the above series of patches are often confluent with the lateral bands. The lack of posterior marginal bands on Abd. V and VI and the failure of the short transverse bands across the mid dorsal line of Abd. IV to join with the parallel longitudinal bands at their extremities are both characteristic of the species.

Material examined.—Seventy-seven samples of *E. intermedia* from 13 counties in England and Wales were examined during the present work. The type specimen in the collection of the British Museum (Natural History) was also examined, with the type specimen of *E. macrocerata.*

Geographical distribution.—*E. intermedia* has been recorded from only two counties in the British Isles in the literature. It is probable that this species has been recorded by many authors as *E. nivalis.* During the present work *E. intermedia* was taken in thirteen counties in England and Wales and was found to be common.

It has not been recorded from any other countries ; the specimen illustrated and described as f. *elongata* by Brook from Austria is probably a specimen of *E. muscorum,* as the figure shows the characteristic triangular shaped marking on Abd. V.

Observation on the habitat.—*E. intermedia* was taken in the more moist habitats of *E. multifasciata,* together with that species. It was especially common on dead vegetation near the ground and on prostrate species of *Cotoneaster* spp.

Entomobrya maritima Reuter

Entomobrya maritima Reuter, 1891, *Medd. Soc. Fauna Fl. fenn.* **18** : 231.
E. lanuginosa var. *maritima* Linnaniemi, 1912, *Acta Soc. Sci. fenn.* **40** : 194.
E. nivalis f. *immaculata* Handschin, 1929, *Die Tierwelt Deutschlands* **16** : 82, *in partem.*

Antennae : Ant. I pale with traces of pale purple pigment at apex ; Ant. II distally pale purple ; Ant. III and IV entirely pale purple.

Head : eye patches black ; triangular black spot between antennal bases only other marking on head.

Thorax, legs and *abdomen* unpigmented.

Variation.—The majority of specimens of this species examined appeared colourless but a few showed traces of a diffuse pale purple pigmentation (fig. 21), and in about 10 per cent. of the specimens examined this pigmentation extended over a large part of the animal (fig. 22). In all the specimens examined, however, the pigment was pale and diffuse. It was most intense on the dorsolateral edges of the segments and along the hind border of the Abd. IV segment, where it formed two lateral spots and a median spot a short distance in front of the posterior border. The median spot was especially characteristic of the species and was present even in specimens with little pigmentation. The pale specimens when examined under high magnification showed traces of the pale purple pigment.

Material examined.—Sixteen samples of *E. maritima* from four counties in England and Wales were examined during the present work.

Geographical distribution.—*E. maritima* has been recorded from nine counties in the British Isles during the course of the present work and in the literature, and has

also been recorded from the following countries :—Germany (Schäffer, 1896) ; Finland (Linnaniemi, 1912) ; Malta (Stach, 1924) and Sweden (Ågren, 1903).

Observations on the habitat of E. maritima.—The specimens taken in the present work were all from a similar type of vegetation, described by Tansley (1939) as a submaritime vegetation and characteristic of spray-washed cliffs. The plants characteristic of this habitat include *Armeria maritima* (Mill.), *Plantago coronopus* L., *P. maritima* L., *Crithmum maritimum* L. and *Festuca rubra* L. The species appears to be common in the above habitat and is essentially a littoral species.

Entomobrya multifasciata (Tullberg)

Degeeria multifasciata Tullberg, 1871, *Öfvers. VetenskAkad. Förh. Stockh.* **28** : 143.
D. muscorum var. *obscura* Tullberg, 1871, *Ibid.* **28** : 143.
D. nivalis Lubbock, 1873, *Monograph of the Collembola and Thysanura.*
Entomobrya nicoleti var. *multifasciata* Börner, 1901, *Abh. naturw. Ver. Bremen.* **17** : 68.
E. nicoleti var. *fasciata* Stach, 1923, *Balkan.-kutat. Tud. Eredm.* **1** : 109.
E. nivalis var. *transiens* Bonet, 1934, *Eos* **9** : 123.
E. nivalis var. *multifasciata* Bonet, 1934, *Ibid.* **9** : 123.
E. nivalis Christiansen, 1958, *Bull. Mus. comp. Zool. Harv.* **118** : 458, *in partem.*

Antennae : Ant. I pale or pale purple, usually with darker purple-black ring at apex ; Ant. II, III and IV pale to dark purple.

Head : eye patches black, connected anteriorly by a band of purple-black, this band continuing back from eyes over dorsolateral surface of head ; anchor-shaped marking usually present on dorsal side of head near posterior margin of segment.

Thorax : Th. I laterally or entirely pigmented with purple-black pigment ; Th. II and III with thin purple-black bands running transversely along posterior margin of segments ; bands may or may not connect with longitudinal lateral bands running from Th. I to posterior margin of Abd. IV ; transverse bands may or may not be broken in the mid-dorsal line.

Legs : pale with a narrow band of purple-black at distal end of femur of metathoracic legs.

Abdomen : Abd. I with narrow band of purple-black running transversely across posterior margin of segment ; Abd. II and III with a pair of purple-black triangular spots situated one each side of mid-dorsal line, the spots joined along posterior margin of segment by a narrow band of the same colour ; Abd. IV with a transverse anterior cross band of purple-black, latter irregular and may be broken in region of mid-dorsal line ; two lateral pigment spots on posterior margin running into longitudinal lateral lines of pigment ; two well developed triangular patches of pigment situated on each side of mid-dorsal line on posterior margin of segment between lateral spots ; these triangular spots may run obliquely forward to join anterior cross band ; bases of triangles may be connected across mid-dorsal line by a short narrow band of pigment ; Abd. V with a band of purple-black pigment running transversely across posterior margin of segment ; Abd. VI with two lateral pigment spots ; manubrium pale.

Variation.—Over 6,000 specimens were examined during the present work and the variation found was between the limits shown in figures 24–31. It consisted largely of reduction or intensification of the density of the pigment, distributed according to the above description. No specimens were observed without pigment or showing reduction further than that depicted in figure 24. The pigment reduction usually resulted in the interruption of the transverse cross band, especially the anterior band on Abd. IV, or the disappearance of the segmental posterior bands, especially those on Abd. II and III ; the reduction stages are shown in figures 24–27. The pigment intensification resulted in the merging of regions of pigment. The spots on Abd. VI join across the anterior margin of the segment, the posterior band of Abd. V broadens, and the lateral posterior spots of Abd. IV merge posteriorly with the triangular spots on the posterior margin of the same segment. The lateral bands develop in the dorsolateral region of the segment and in extreme specimens merge into the triangular spots of Abd. II and III and with the hind bands of Th. II–Abd. I as in figure 31. This extreme development of pigmentation is rather uncommon in the field and the majority of specimens examined corresponded to figures 25–27. The anchor shaped mark on the

head extends in intensely pigmented specimens into a longitudinal line running along the mid dorsal line of the head, and in these examples the mesothoracic and prothoracic legs frequently have a narrow band of purple-black pigment at the distal end of the femur.

The triangular spots on the hind margin of Abd. IV are very characteristic of this species and were clearly marked on most specimens examined. Where these spots were joined to the anterior cross band the connectives ran from the apex of the triangle only.

Material examined.—Over 200 samples of *E. multifasciata* from 15 counties in England and Wales were examined during the present work. Material was also examined from France, Germany, Switzerland and U.S.A.

Geographical distribution.—*E. multifasciata* has been recorded from 43 counties in the British Isles during the present work and in the literature, and from the following countries :—Albania (Stach, 1923) ; Argentina (Bonet, 1934) ; Australia (Womersley, 1936) ; Austria (Torne, 1958) ; Canada (Hammer, 1953) ; Czechoslovakia (Rambousek, 1928) ; Finland (Linnaniemi, 1912) ; Germany (Schäffer, 1896) ; Hungary (Stach, 1922) ; Italy (Brook, 1884) ; Japan (Uchida, 1954) ; Juan Fernandez (Schött, 1921) ; Iceland (Hammer-Jorgensen, 1938) ; Madeira (Agrell, 1939) ; Mongolia (Yosii, 1949); Poland (Schubert, 1933); Portugal (Da Gama, 1959); Russia (Kryukova, 1932) ; Sweden (Ågren, 1903) ; Switzerland (Handschin, 1924) ; U.S.A. (Wray *et al.*, 1950).

Observations on the habitat.—*E. multifasciata* was taken most frequently on the ground in the present work. It was common on litter, especially that of coniferous trees, and under dead vegetation and low growing plants on arable land, where it was also taken on bare soil. Some specimens were taken from low shrubs, for example *Cotoneaster* spp. and *Ulex europaeus* L., and from the bark at the base of tree trunks, but the largest numbers were found in samples taken from the ground.

Entomobrya muscorum (Nicolet)

Degeeria muscorum Nicolet, 1841, *N. Denkschr. schweiz. Ges. Naturw.* **6** : 74, *nec* Tullberg, 1871. *E. nivalis* Christiansen, 1958, *Bull. Mus. comp. Zool. Harv.* **118** : 457, *in partem.*

Antennae : all segments tinged with pale purple ; apex of Ant. IV dark purple.

Head : eye patches black, joined anteriorly by a purple band which extends dorsolaterally across head on each side ; patch of pigment present in some specimens on dorsal side of head in mid-dorsal line.

Thorax : pair of lateral bands running from anterior margin of Th. II to posterior margin of Th. III ; pair of dorsolateral bands running one each side of mid-dorsal line from anterior border of Th. II to posterior border of Abd. III.

Legs : tibiotarsus of prothoracic leg may be tinged with purple, in other legs pale ; femur of all legs with some purple coloration and with a band of purple-black at apex.

Abdomen : pair of dorsolateral bands running one each side of mid-dorsal line from anterior border of Th. II to posterior border of Abd. III, these bands expanding into two triangular-shaped patches on Abd. III, joined along posterior margin of Abd. III by a narrow pigment band ; there may be a pair of lateral pigment spots on Abd. III ; Abd. IV with a band of pigment along posterior margin of segment, band frequently broader laterally ; pair of longitudinal parallel bands of even thickness arising from posterior marginal band and running towards anterior margin of segment, forking about half way along segment into two branches, one branch running obliquely forward to join anterior margin in a well developed patch of pigment laterally, the other running to mid-dorsal line of segment where it joins its opposite number at a point just posterior to anterior border of Abd. IV, the two forming a characteristic inverted V-shaped marking. Abd. V with a triangular spot in mid-dorsal line of segment, base along posterior margin of segment and apex reaching almost to anterior border of segment ; Abd. VI with no pigment.

Variation.—The parallel bands on Abd. IV are often poorly developed in the posterior half of the segment. The lateral branch of these bands is always well developed but the inner band is frequently poorly developed or occasionally missing.

Material examined.—Only two samples of *E. muscorum*, consisting of 11 specimens, were examined. The samples were from Switzerland.

Geographical distribution.—*E. muscorum* has been recorded in the literature from 14 counties in the British Isles but, since it has frequently been confused with *Degeeria muscorum* Tullberg, 1871, the records are probably suspect. The species has been recorded from the following countries :—Albania (Stach, 1923); Argentina (Bonet, 1934); Austria (Torne, 1958); Canada (Hammer, 1953); Germany (Börner, 1901); Hungary (Stach, 1922); Madeira (Agrell, 1939); Poland (Schubert, 1933) and Switzerland (Gisin, 1947).

Entomobrya nicoleti (Lubbock)

Degeeria nicoleti Lubbock, 1868, *Trans. Linn. Soc. Lond.* **26** : 295.
D. muscorum Tullberg, 1871, *Öfvers. VetenskAkad. Förh. Stockh.* **28** : 143, *in partem.*
Entomobrya multifasciata var. *nicoleti* Brook, 1884, *J. Linn. Soc. Lond.* (*Zool.*) **17** : 278.
E. muscorum var. *nicoleti* Schäffer, 1896, *Mitt. naturh. Mus. Hamb.* **13** : 150.
E. lanuginosa ab. *nicoleti* Ågren, 1903, *Stettin. ent. Ztg.* **64** : 113.
E. nivalis Handschin, 1929, *Die Tierwelt Deutschlands* **16** : 82, *in partem.*

Antennae : Ant. I and II pale, ringed apically with purple black ; Ant. III and IV pale purple, former often with apical ring of purple-black ; antennae frequently darker purple, then Ant. I and II pale to dark purple.

Head : eye patches black, joined anteriorly by a narrow purple-black band, extending back from eyes over dorsolateral surface of head.

Thorax : Th. II and III with a little purple-black pigment laterally.

Legs unpigmented.

Abdomen : Abd. I, II and III unpigmented. Abd. IV with two pairs of purple-black spots situated along posterior margin of segment and on either side of mid-dorsal line (fig. 16) ; outer pair of spots situated in lateral extremities of tergum of Abd. IV; Abd. V with a continuous purple-black band along posterior margin of segment ; Abd. VI unpigmented.

Variation.—Figures 16–19 show the wide range of variation found in this species. The darker forms are rare and only two specimens as heavily pigmented as figure 19 were found during the present work. Forms similar to that figured in figure 18 comprised about 20 per cent. of the specimens examined, although the actual proportion varied considerably and samples containing only the forms shown in figures 16 and 17 were common. The proportion of dark forms present did not appear to be correlated with the season or habitat. The intensification of pigment distribution first takes the form shown in figure 17, where a pair of irregular thin processes develops forward from the inner pair of spots on Abd. IV. These processes extend towards the lateral margins of the segment and enlarge to join the lateral bands of pigment which are present in the more heavily pigmented forms. This stage is shown in figure 18. In forms similar to that in figure 19 the lateral bands extend on to the dorsolateral surface of Abd. I, II and III. In the forms normally found in samples (figs. 16–18) the extensions of the lateral bands dorsolaterally never reach the mid dorsal line of the segment. Even in figure 19 the transverse bands along the posterior margin of Abd. II and III are only very weakly developed. The presence of two pairs of spots on the posterior margin of Abd. IV is characteristic of the forms in figures 16–17. The diffuse development of the pigment and the absence of well defined markings are characteristic of more heavily marked specimens as also is the lateral filling of the posterior extremities of the terga of Abd. I, II and III in the absence of any cross bands on the segments.

Material examined—One hundred and twenty-two samples of *E. nicoleti* from 14 counties in Scotland, England and Wales were examined during the present work. Material was also examined from Germany and France.

Geographical distribution.—*E. nicoleti* has been recorded from 32 counties in the British Isles during the course of the present work and in the literature, and from the

following countries :—Albania (Stach, 1923) ; Finland (Linnaniemi, 1912) ; Germany (Schäffer, 1896) ; Hungary (Stach, 1922) ; Malta (Stach, 1924) ; and Sweden (Ågren, 1903).

Observations on the habitat.—This species is characteristic of rough grassland, and was especially common in tussocks of *Dactylis glomerata* L. *E. nicoleti* was taken in small numbers from the lower branches of shrubs and from dead vegetation.

Entomobrya nivalis (L.)

Podura nivalis Linnaeus, 1758, *Systema Naturae*, ed. 10 : 608.
P. nigromaculata Templeton, 1835, *Trans. ent Soc. Lond.* **1** : 94.
Degeeria nivalis Nicolet, 1841, *N. Denkschr. schweiz. Ges. naturw.* **6** : 71.
D. annulata Lubbock, 1873, *Monograph of the Collembola and Thysanura* : 236.

The following varieties are considered by the present author to be synonyms with *E. nivalis* :—

E. nivalis var. *immaculata* Schäffer, 1896, *Mitt. naturh. Mus. Hamb.* **13** : 150.
E. nivalis var. *maculata* Schäffer, 1896, *Ibid.* : 149.
E. nivalis var. *pallida* Schäffer, 1896, *Ibid.* : 150.
E. nivalis ab. *dorsalis* Ågren, 1904, *Ark. Zool.* **2** : 26 ; *nec.* Uzel, 1891.
E. nivalis var. *torquata* Navas, 1906, *Broteria* **5** : 145.
E. nivalis var. *atrata* Stach, 1920, *Bull. int. Acad. Cracovie* (*Acad. pol. Sci.*) (1919) **1920** : 133.
E. nivalis var. *abrupta* Stach, 1924, *Ann. hist.-nat. Mus. nat. hung.* **21** : 105.

Antennae : all segments pale, tinged with pale purple-black pigment, rarely darker ; very slight intensification of pigment at distal ends of antennal segments.

Head, thorax and *legs :* as *E. multifasciata.*

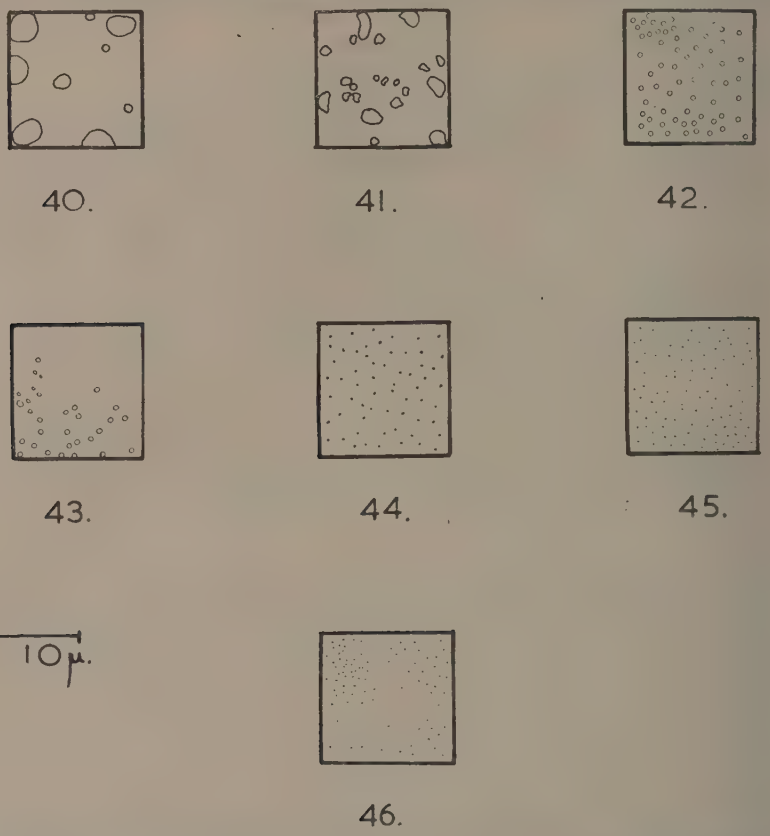
Abdomen : Abd. I, II and III as *E. multifasciata* ; Abd. IV with a pair of lateral patches of pigment at posterior margin of segment, as in *E. multifasciata* and a narrow band of pigment running along posterior margin of segment between the two lateral patches, frequently meeting them at its extremities ; a pair of parallel longitudinal bands of even thickness arising from this band on each side of the mid-dorsal line, these bands running half length of segment before terminating ; from apex of these bands an oblique band running to meet lateral band at anterior margin of segment ; Abd. V and VI as *E. multifasciata.*

Variation.—*E. nivalis* shows considerable variation. This, as in other *Entomobrya*, is due to the reduction or intensification of the pattern pigment.

Intensification of the pattern results in the extension of the apices of the parallel bands on Abd. IV laterally to meet in the mid dorsal line. This process differs from that in *E. muscorum*, since in the former the connecting band never extends forward into the anterior half of the segment and is therefore straight and not V-shaped. The band is usually incomplete in the centre, as in figure 38 ; further intensification results in the joining of the bands and then in extreme forms the area between the parallel lines becomes pigmented. These forms probably correspond to f. *dorsalis* Ågren. While the slight intensification (fig. 38) is quite frequent in populations, up to 27 per cent. of a population being recorded, the form in figure 39 is rarer, occurring in only 3–5 per cent. of most populations.

A complete series of reduction stages occurs in *E. nivalis*. The posterior transverse pigment bands disappear from the anterior segments (figs. 34 and 35) and the remaining pigment then goes, leaving a pair of lateral spots on the posterior border of Abd. IV (fig. 33). The spots are reduced in some specimens to the condition in figure 32, and one pigmentless specimen was recorded during this work. The form in figure 33 probably corresponds to var. *maculata* Stach and is uncommon, occurring in about 2–4 per cent. of the specimens taken on *Ulex europaeus* and 7–13 per cent. of the speci-

mens examined from under bark. The forms in figures 34 and 35 probably correspond to var. *pallida* Schäffer and occur quite commonly under bark (up to 50 per cent. of the specimens examined) although it was less common on shrubs (1–18 per cent. on *Ulex*). The form in figure 33 frequently shows traces of the parallel bands of the f.p. colour pattern when examined under reflected light. The single pair of pigment patches on Abd. IV in reduced pigment forms distinguishes this species from other pale species, i.e. *E. nicoleti* and *E. maritima*. The form of the parallel bands on Abd. IV



Figs. 40–46.—Sculpture of the chorion of eggs of the genus *Entomobrya* (pattern shown in squares of 15 μ sides): (40) *E. corticalis*; (41) *E. nicoleti*; (42) *E. albocincta*; (43) *E. maritima*; (44) *E. multifasciata*; (45) *E. nivalis*; (46) *E. intermedia*.

characterises the normal form of this species. The pigmentless form can only be distinguished from *E. maritima*, the other pigmentless species, by the presence in the latter of purple pigmentation under high magnification.

Material examined.—One hundred and seventy-six samples of *E. nivalis* from 16 counties in England, Wales and Scotland were examined during the present work. Material was also seen from Austria, France, Germany, Switzerland and U.S.A.

Geographical distribution.—*E. nivalis* has been recorded from 54 counties in the British Isles in the present work and in the literature, and from the following countries: —Argentina (Bonet, 1934); Australia (Womersley, 1936); Austria (Torne, 1958); Czechoslovakia (Paclt, 1956); Egypt (Hargreaves, 1948); Faroes (Hammer, 1953); France (Trave, 1954); Finland (Linnaniemi, 1912); Germany (Schäffer, 1896);

Hungary (Stach, 1922); Iceland (Hammer-Jorgensen, 1938); Italy (Brook, 1884); Japan (Uchida, 1954); Malta (Stach, 1924); New Zealand (Womersley, 1936); Norway (Lie-Petersen, 1900); Poland (Schubert, 1933); Sweden (Ågren, 1903); Switzerland (Gisin, 1947); Siberia (Hammer, 1953); U.S.A. (Christiansen, 1958*a*).

Observations on the habitat.—*E. nivalis* was found on shrubs and on the bark of trees. The species was very common on 14 species of shrub, especially *Ulex europaeus*, and was found most frequently on the older mature foliage where the branches supported an extensive flora of Fungi Imperfecti. Specimens were taken from the bark of 14 species of tree, the insect occurring usually on the surface of the bark. *E. nivalis* was found in smaller numbers on low vegetation, including *Clematis vitalba* L. and *Rubus* sp.

Entomobrya pulchella (Ridley)

Degeeria pulchella Ridley, 1881, *Ent. mon. Mag.* **17** : 270.
Entomobrya multifasciata Brook, 1884, *J. Linn. Soc. Lond.* (*Zool.*) **17** : 276.

Antennae : Ant. I and II pale, latter with an apical blue-black band; Ant. III and IV pale blue-black.

Head : eye patches black, connected by a band of blue-black pigment which extends to sides of head; remainder of head pale.

Thorax : Th. II ringed on all borders by band of blue-black pigment; (Th. III black).

Legs : (white with black articulations).

Abdomen : (Abd. I yellow, Abd. II black, Abd. III yellow); Abd. IV with a broad transverse band of blue-black pigment running anteriorly across the segment; this band may be broken in mid-line; an irregular broad band also running across posterior margin of segment; Abd. V with a narrow posterior band; Abd. VI pale.

Variation.—Only three specimens were available for examination and unfortunately these were damaged, especially in the thoracic and anterior abdominal region. The above diagnosis includes portions quoted from Ridley's original description where the material was not clearly visible, and these quotations are placed in brackets. No apparent variation was observed in the specimens examined.

Other characters.—The empodial appendage was clearly serrated posteriorly and this is illustrated by Handschin (1929 : 77, fig. 141).

Material examined.—Only one sample of *E. pulchella*, consisting of three mature specimens, was examined. The sample was from Switzerland.

VI. The Immature Stages of the British Species of *Entomobrya*

(1) *The Egg*

General description

The egg when first laid is white, opaque, smooth and spherical, with a diameter of 0·15–0·19 mm. The chorion breaks after two days at 17° C. and the egg rapidly increases in size to 0·24 mm. At this stage the egg is a dirty white colour and oval in shape; the outer chorion forms two caps which adhere to the egg throughout its development, and a number of filaments appear on the surface of the inner chorion. No further increase in size takes place until the eighth day when the egg increases to 0·26–0·27 mm.; at this stage the egg is purple-brown and the eyes of the insect are visible. Hatching occurs without further external change on the tenth or eleventh day after laying. The filaments do not appear to be specific and, in the seven species examined, were about 0·05 mm. to 0·10 mm. long and between 40–60 in number. It was found that the sculpturing of the outer chorion caps is specific, consisting of small round processes or granular reticulations. These were counted in areas of 15 μ sides and the count for each species is given below.

Specific Description

E. albocincta (fig. 42).—Processes small, regular and rounded, none with diameter exceeding 0·5 μ; count: mean 57·6, limits 45–72; chorion appears rough under low power.

E. corticalis (fig. 40).—Processes large, mostly rounded, a few elliptical, between 1–4 μ in diameter; count: mean 8·6, limits 6–13; chorion appears rough under low power.

E. maritima (fig. 43).—Processes similar to *E. albocincta*, probably a little smaller; count: mean 33·1, limits 30–38; strongly aggregated and with some areas bare; chorion appears smooth under low power.

E. multifasciata (fig. 44).—No processes, but chorion with reticulations, regular in size and arrangement; count: mean 68·4, limits 45–108; chorion appears smooth under low power.

E. intermedia (fig. 46).—As *E. multifasciata* but reticulations finer; count: mean 174·0, limits 165–195.

E. nicoleti (fig. 41).—Processes irregular, largely rounded and rarely larger than 2 μ in diameter, a few elongated and reaching up to 3–4 μ in length; count: mean 22·9, limits 17–28; chorion rough under low power.

E. nivalis (fig. 45).—As *E. multifasciata* but reticulations intermediate between this species and *E. intermedia* in size; count: mean 112·5, limits 90–135.

A series was observed in the size of the markings between *E. multifasciata*, *E. nivalis* and *E. intermedia*, all reticulated forms. Those of *E. multifasciata* appear coarse and those of *E. intermedia* fine, with *E. nivalis* intermediate between them.

(2) *The Immature Instars*

The immature instars were those recorded before sexual maturity; in *Entomobrya* the number was five. Little morphological differentiation was observed between the first and mature instars; there were some changes in relative proportions, *e.g.* in antennal segment ratios, but these were found to be very variable and of little quantitative use. It was found, however, that the immature instars could be separated by the use of two characters, the retinaculum and the trochanteral organ, and that this separation was of practical application in the course of the present work.

The retinaculum in instars other than the first has a single, large seta arising from the anterior face of the corpus and often extending to the apex of the ramus (fig. 7). The seta is absent in the first instar of the six species examined (fig. 6). Figure 47 shows a generalised diagram of the trochanteral organ of *Entomobrya*, using the terminology of Christiansen (1958*a*). The organ is on the ventral face of the trochanter of the metathoracic leg, the apical seta being situated in the posterior distal angle of the segment. The organ consists of an apical seta, two rows of setae arising from this point (posterior and ventral arms), an outer row of external setae and a group of internal setae. The rows of setae are always distinct from the other setae: if the distance between the setae of the posterior arm is x then it was found that the distance between the most distal seta of the arm and the nearest internal seta was at least $2x$. Similarly in the case of the distal seta of the ventral arm and the seta marked a; the latter appeared to be a member of the row of external setae. Little variation was observed in the arrangement of the setae of the trochanteral organ in the immature stages, although considerable variation occurred in subsequent instars. It is proposed to use the following formula for describing the trochanteral organ in the descriptions of instars below:

> apical seta/ventral arm/posterior arm/external seta/internal setae; thus for the organ illustrated in figure 47 the setal arrangement is:—1/4/5/3/3, with the seta a excluded.

The genital plate appears in the sixth instar although in three specimens a female plate was observed in the fifth instar. The region of the genital plate is frequently raised from the surrounding area into a papilla-like structure in the fifth instar but no other differentiation was observed. The pattern pigment appears towards the end of

the first instar and the pattern is therefore complete in form from the second instar onwards, although some intensification of the markings takes place throughout life.

The development of the trochanteral organ is shown in figures 48–57. In the first and second instars the organ is represented only by the apical seta (fig. 48). In the third instar the organ consists of an apical seta, one seta in each of the posterior and ventral arms and one external seta. In the first three instars no variation in pattern has been observed but in the fourth instar (figs. 50 and 51) the organ consists of the apical seta, one or two setae in the ventral arm, two setae in the posterior arm and two external setae. The fifth instar organ consists of an apical seta, two or three setae in the ventral arm, three setae in the posterior arm and two external setae. The trochanteral organ is therefore relatively simple in form in the immature stages of *Entomobrya* ; the apical seta occupies a constant position and is the largest seta of the organ,

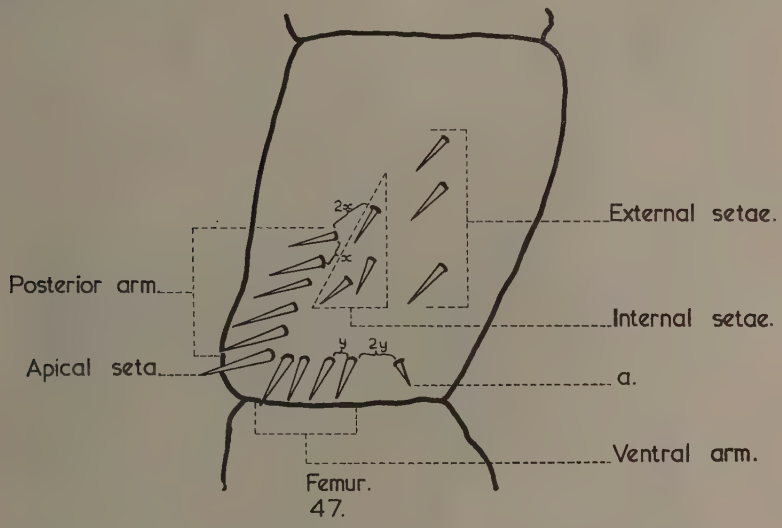
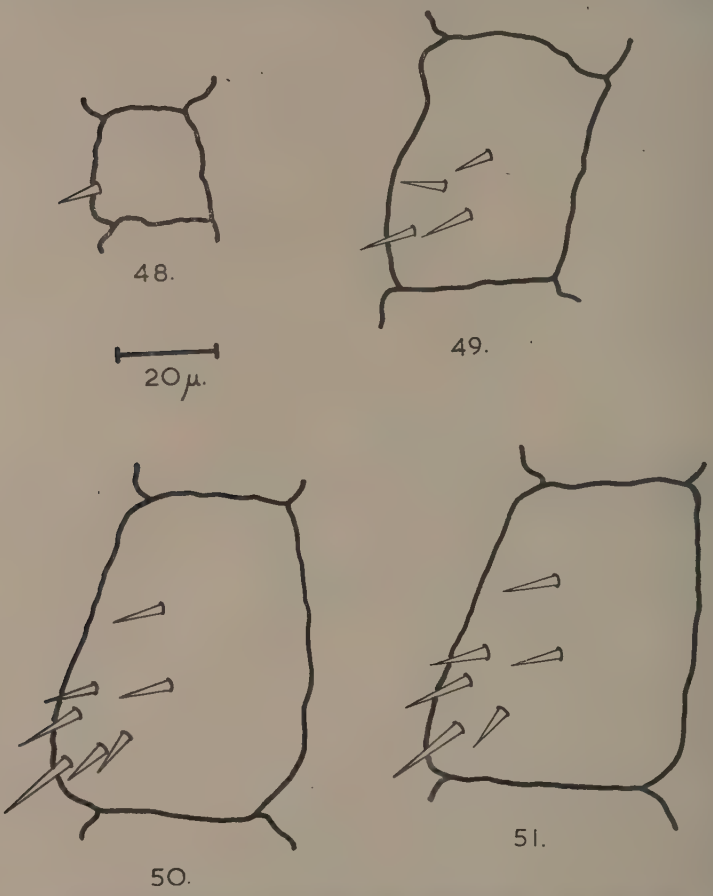


Fig. 47.—Generalised diagram of trochanteral organ in the genus *Entomobrya*.

the ventral and posterior rows lengthen by one spine at each ecdysis in a direction away from the apical seta and the external setae increase by two spines. The spines in the two rows decrease in order of size along the rows from the apical setae. No internal setae have been observed in the immature stages. The angle between the arms of the organ varies with distortion on mounting, but is between 35° and 60°. In the mature instars the posterior and ventral arms continue to increase by increments of one spine in the earlier instars (*c.f.* figs. 54–56, of the sixth to eighth instars) but the increment is frequently missed and in later instars the number of spines in the rows is usually rather lower than would be expected if the increase was constant. It is therefore difficult to age mature specimens by the trochanteral organ. Figure 57 shows the arrangement of the trochanteral organ in the fourteenth instar and the rows number only 8 and 9 spines instead of the expected 11 and 12 spines. The external setae form a row of spines running across the base of the triangle formed by the two arms. They number two spines up to the fifth instar but one further spine is added at the proximal end of the row in the sixth instar and the number of three spines in the external seta row then remains constant throughout the remainder of development of the organ, although sometimes the external row may number only two spines in mature specimens. The spine marked *a* in figure 47 appears to belong to the external seta row, although at the end of the ventral row, but its occurrence is rather erratic

in the specimens examined. The arrangement of the internal setae is very variable and although none were observed in the immature specimens they do not appear to be related to the age of the insect in the mature instars. The number varied from one spine in the sixth instar and 0–3 in the seventh instar to 11–15 in the fourteenth instar, and the arrangement of the spines did not appear to follow any pattern.



Figs. 48–51.—The trochanteral organ in *Entomobrya multifasciata*: (48) first instar; (49) third instar; (50–51) fourth instar, two alternative setal arrangements.

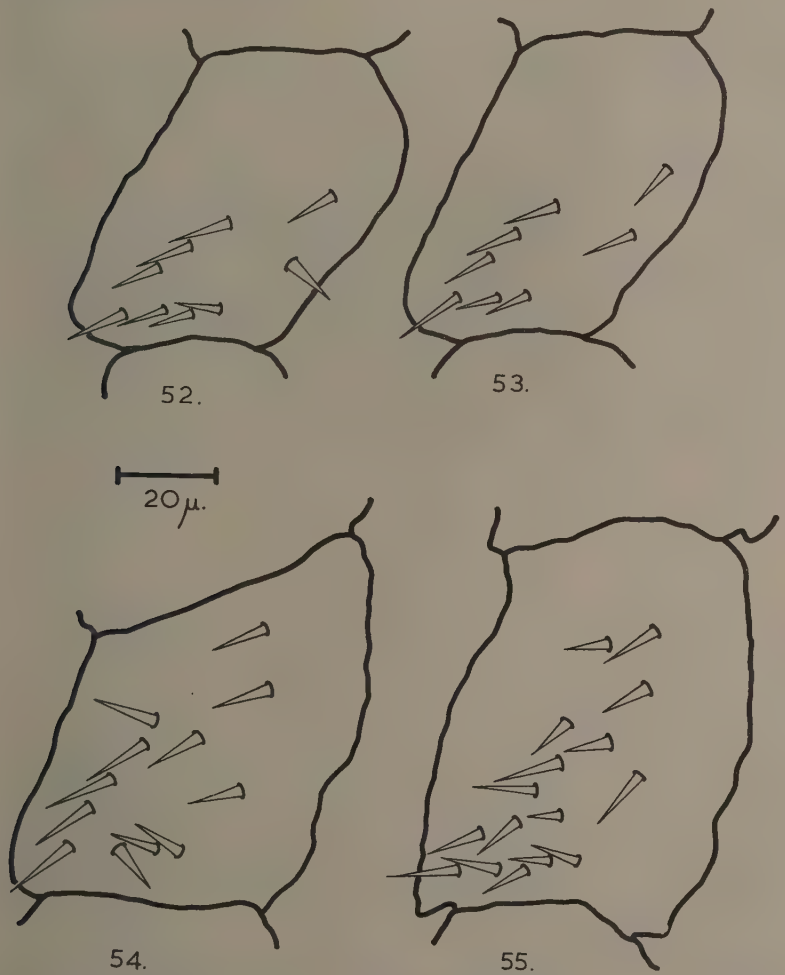
The measurements and the formula characterising the trochanteral organ of the immature instars of the British *Entomobrya* examined are summarised below, variation of the trochanteral organ being expressed as a percentage of the number of legs examined. The body length and cephalic diagonal measurements are given in mm. as a mean of the measurements taken, the observed limits being given in brackets. The body length is taken from the anterior margin of Th. II to the posterior margin of Abd. VI and both measurements were made on unmounted specimens in alcohol using a low power microscope. Twenty specimens of each instar for each species have been examined, all reared under laboratory conditions. Body length, cephalic diagonal measurement and formula characterising the trochanteral organ are given in that order.

E. albocincta

First instar : 0·33 (0·29–0·37) ; 0·14 (0·12–0·18) ; 1/0/0/0/0, no variation. *Second instar :* 0·40 (0·37–0·45) ; 0·15 (0·13–0·17) ; 1/0/0/0/0, no variation. *Third instar :* 0·51 (0·44–0·55) ; 0·17 (0·15–0·18) ; 1/1/1/1/0, no variation. *Fourth instar :* 0·61 (0·47–0·77) ; 0·20 (0·18–0·22) ; 1/1/2/2/0 70 per cent., 1/2/2/2/0 30 per cent. *Fifth instar :* 0·71 (0·59–0·82) ; 0·23 (0·20–0·24) ; 1/2/3/2/0 57 per cent., 1/3/3/2/0 43 per cent.

E. corticalis

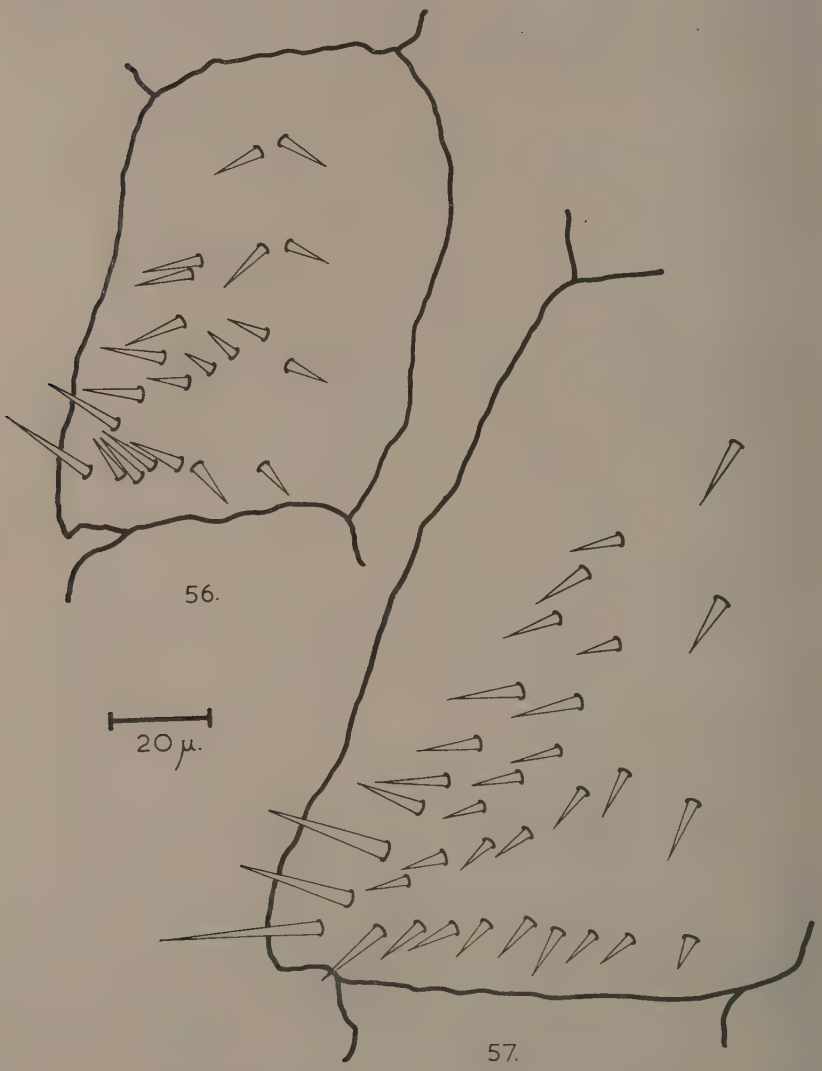
First instar : 0·37 (0·30–0·44) ; 0·14 (0·13–0·15) ; 1/0/0/0/0, no variation. *Second instar :* 0·50 (0·47–0·57) ; 0·17, no variation ; 1/0/0/0/0, no variation. *Third instar :* 0·69 (0·55–0·80) ; 0·20 (0·18–0·21) ; 1/1/1/1/0, no variation. *Fourth instar :* 0·79 (0·64–0·87) ; 0·21 (0·18–0·24) ; 1/1/2/2/0 53 per cent., 1/2/2/2/0 45 per cent. *Fifth instar :* 0·92 (0·80–1·17) ; 0·26 (0·22–0·30) ; 1/2/3/2/0 59 per cent., 1/3/3/2/0 37 per cent. ; two abnormal trochanteral organs with spine arrangements 1/3/2/2/0 and 1/3/4/2/0.



FIGS. 52–55.—The trochanteral organ in *Entomobrya multifasciata* : (52–53) fifth instar, two alternative arrangements; (54) sixth instar, one of alternative spine arrangements. (55) later mature instar.

E. multifasciata

First instar : 0·40 (0·34–0·47) ; 0·15 (0·12–0·17) ; 1/0/0/0/0, no variation. *Second instar :* 0·52 (0·45–0·57) ; 0·17 (0·15–0·18) ; 1/0/0/0/0, no variation. *Third instar :* 0·66 (0·49–0·77) ; 0·20 (0·18–0·22) ; 1/1/1/1/0, no variation. *Fourth instar :* 0·75 (0·64–0·91) ; 0·23 (0·20–0·29) ; 1/1/2/2/0 53 per cent., 1/2/2/2/0 44 per cent.; one abnormal trochanteral organ with spine arrangement of 1/2/3/2/0. *Fifth instar :* 1·02 (0·91–1·14) ; 0·29 (0·27–0·32) ; 1/2/3/2/0 79 per cent.. 1/3/3/2/0 16 per cent.; two abnormal trochanteral organs with spine arrangements 1/2/4/2/0 and 1/4/3/2/0.



Figs. 56–57.—The trochanteral organ in *Entomobrya multifasciata*, later mature instars.

E. intermedia

First instar : 0·40 (0·32–0·47) ; 0·15 (0·12–0·17) ; 1/0/0/0/0, no variation. *Second instar :* 0·53 (0·42–0·62) ; 0·18 (0·15–0·18) ; 1/0/0/0/0, no variation. *Third instar :* 0·65 (0·52–0·77) ; 0·21 (0·18–0·22) ; 1/1/1/1/0, no variation. *Fourth instar :* 0·79 (0·55–0·97) ; 0·24 (0·20–0·27) ; 1/1/2/2/0 31 per cent., 1/2/2/2/0 65 per cent. ; one abnormal trochanteral organ with spine arrangement 1/3/2/2/0. *Fifth instar :* 0·96 (0·84–1·14) ; 0·28 (0·25–0·32) ; 1/2/3/2/0 30 per cent., 1/3/3/2/0 65 per cent. ; one abnormal trochanteral organ with spine arrangement 1/2/2/2/0.

E. nicoleti

First instar : 0·31 (0·27–0·35) ; 0·12 (0·10–0·13) ; 1/0/0/0/0, no variation. *Second instar :* 0·44 (0·40–0·47) ; 0·15 (0·13–0·17) ; 1/0/0/0/0, no variation. *Third instar :* 0·53 (0·49–0·60) ; 0·17 (0·15–0·18) ; 1/1/1/1/0, no variation. *Fourth instar :* 0·65 (0·54–0·70) ; 0·20 (0·18–0·22) ; 1/1/2/2/0 89 per cent., 1/2/2/2/0 11 per cent. *Fifth instar :* 0·78 (0·60–0·94) ; 0·23 (0·20–0·27) ; 1/2/3/2/0 98 per cent., 1/3/3/2/0 0 per cent. ; one abnormal trochanteral organ with spine arrangement of 1/1/3/2/0.

E. nivalis

First instar : 0·34 (0·30–0·39) ; 0·13 (0·12–0·15) ; 1/0/0/0/0, no variation. *Second instar :* 0·46 (0·40–0·52) ; 0·17 (0·15–0·18) ; 1/0/0/0/0, no variation. *Third instar :* 0·64 (0·54–0·74) ; 0·21 (0·20–0·22) ; 1/1/1/1/0, no variation. *Fourth instar :* 0·82 (0·64–0·97) ; 0·23 (0·20–0·30) ; 1/1/2/2/0 40 per cent., 1/2/2/2/0 60 per cent. *Fifth instar :* 0·94 (0·67–1·14) ; 0·28 (0·22 -0·30) ; 1/2/3/2/0 71 per cent., 1/3/3/2/0 29 per cent.

Sexually mature *Entomobrya* continue to increase in size after each moult ; the size increments are, however, smaller and the maximum size recorded for specimens taken in the field are : *E. multifasciata*, *E. intermedia* and *E. nivalis* : 2·0–2·5 mm.; *E. albocincta*, *E. corticalis*, *E. maritima* and *E. nicoleti* : 1·4–1·5 mm.

The variation of spine arrangement noted above in several instances was rare and in every case it was found that the other metathoracic leg of the specimen was typical of the instar. When a specimen examined was near ecdysis, the trochanteral organ was visible through the cuticle of the trochanter.

The variation in the trochanteral organ of the fourth and fifth instars observed above resembles that found in specimens taken in the field. The following table shows the percentage variation in these instars for *E. multifasciata*, taken from cedar needle litter, and for specimens of this species reared in the laboratory :—

Instar	Trochanteral organ	Percentage variation in specimens	
		Field	Laboratory
Fourth instar .	1/1/2/2/0	51	53
	1/2/2/2/0	49	44
Fifth instar .	1/2/3/2/0	73	79
	1/3/3/2/0	27	16

VII. Key to the Immature Stages of the British *Entomobrya*

1 (4) Trochanteral organ with apical spine only, *i.e.* 1/0/0/0/0.
2 (3) Retinaculum without seta on the corpus (fig. 6) . . . . . *First instar*
3 (2) Retinaculum with seta on the corpus (fig. 7) . . . . . *Second instar*
4 (1) Trochanteral organ with more than one spine.
5 (6) Trochanteral organ with four spines, 1/1/1/1/0 . . . . . *Third instar*
6 (5) Trochanteral organ with more than four spines.
7 (8) Trochanteral organ with more than nine spines, genital plate well developed . . . . . *Mature instars**
8 (7) Trochanteral organ with five to nine spines, genital plate absent or poorly developed.
9 (10) Trochanteral organ either 1/1/2/2/0 or 1/2/2/2/0 . . . . . *Fourth instar*
10 (9) Trochanteral organ either 1/2/3/2/0 or 1/3/3/2/0 . . . . . *Fifth instar*

* Mature instars : sexually mature instars, *i.e* sixth and subsequent instars.

VIII. A Comparative Study of the Effect of Two Physical Factors on Some *Entomobrya*

(1) *Relative Humidity*

A study of the mortality rates of six species of *Entomobrya* at six different relative humidities was made, using the technique of Davies (1929). The insects were exposed to the following relative humidities at 24° C.: 0 per cent., 10 per cent., 20 per cent., 50 per cent., 70 per cent., 90 per cent., 95 per cent. and 100 per cent., the range of relative humidities being obtained by using an A.R. sulphuric acid/distilled water mixture in the proportions of acid to water given by Solomon (1951). The values of the relative humidities between 20 per cent. and 90 per cent. were checked with a Gregory Hygrometer.

The experiments were carried out in later winter and early spring, on material taken directly from the field ; this ensured that the majority of the individuals used were mature, any obviously immature cases being removed. Twenty-five individuals of each species were exposed to each relative humidity in batches of five, one batch of each species being exposed at one time. The results are given in Table I.

Table I.—*The mean length of life at different relative humidities of five species of* Entomobrya *compared with that of* E. nicoleti. *Mean lengths of life are expressed as a ratio, taking that of* E. nicoleti *as* 1·0

(a. *E. nicoleti* ; b. *E. albocincta* ; c. *E. corticalis* ; d. *E. multifasciata* ; e. *E. intermedia* ; f. *E. nivalis*.)

Percentage R.H.	a.	b.	c.	d.	e.	f.
0	1·0	2·3	3·0	1·1	2·6	1·9
10	1·0	2·1	1·3	1·2	1·3	1·8
20	1·0	1·8	1·8	1·3	1·1	1·7
50	1·0	1·4	1·6	1·4	1·1	1·6
70	1·0	1·9	1·8	2·3	1·6	2·9
90	1·0	1·4	2·5	2·1	1·1	1·7
95	1·0	1·0	1·7	1·8	1·0	2·4
100	Discontinued at 214 hours					
Mean	1·0	1·7	2·0	1·6	1·4	2·0

(2) *Carbon Dioxide*

It has been noted above that *Entomobrya* can be anaesthetised with carbon dioxide gas. It was observed during the course of the present work that the recovery speed of the insect varied with the species and a series of experiments were undertaken to investigate this phenomenon. A sample, consisting of 20 specimens of each species, was made up in a pooter (*see* Petersen, 1947 : plate 68, fig. 8) in the field in early spring ; all the specimens were therefore probably mature. Four similar samples were taken using individuals from other habitats. A total of 100 individuals of each species was therefore tested in the experiments. The pooter was attached to a carbon dioxide cylinder and a standard dose passed through it, through a valve. The anaesthetised Collembola were tipped on to a piece of moist filter paper under a low power microscope and the number of each species recovering in each minute recorded with the aid of a stop watch.

Figure 58 shows the rate of recovery for each species, represented by the total recovery in each minute for the five replicates expressed as a percentage of the total specimens of each species. Table II shows the mean weight with limits of a representative sample of 20 specimens of each species.

TABLE II.—*Mean weight of a representative sample (20 specimens) of six species of* Entomobrya

Species	Mean weight (mg.)	Limits (mg.)
E. albocincta	0·13	0·09–0·19
E. corticalis	0·11	0·07–0·13
E. multifasciata	0·22	0·12–0·32
E. intermedia	0·25	0·13–0·46
E. nicoleti	0·17	0·08–0·22
E. nivalis	0·25	0·16–0·33

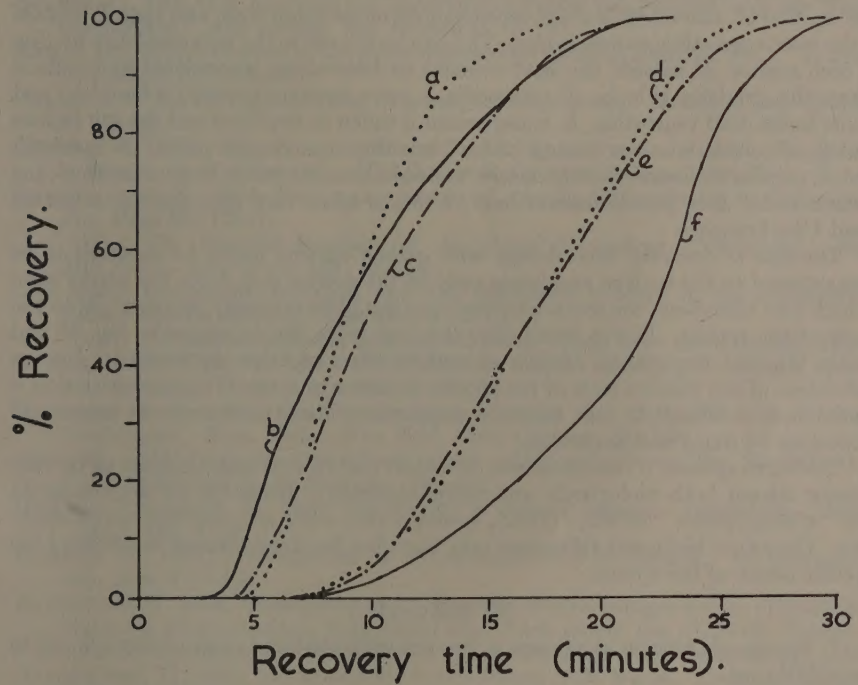


FIG. 58—Graph showing rate of recovery of some *Entomobrya* after anaesthetisation by carbon dioxide gas: *a*, *E. intermedia*; *b*, *E. nivalis*; *c*, *E. multifasciata*; *d*, *E. nicoleti*; *e*, *E. albocincta*; *f*, *E. corticalis*.

IX. DISCUSSION

The variation in pattern and absence of other morphological differences in most *Entomobrya* has led to an extensive synonymy for the genus in the major works on collembolan systematics and as a result of this synonymy the specific status of some of the forms has been questioned. Some authors, *e.g.* Tullberg (1872) and Linnaniemi (1912), considered that the forms were true species while others, *e.g.* Bonet (1934) and Christiansen (1958*a*), considered that all the forms were varieties of one species, *E. nivalis*.

Mayr *et al.* (1953) defined species as "groups of actually (or potentially) interbreeding natural populations which are reproductively isolated from other such groups". It was not possible to verify this criterion experimentally during the present work, as the sexing of living *Entomobrya* was impossible. Cultures of *Entomobrya* taken in the field in no instance laid eggs that gave rise to forms other than the species in the culture, and some of the above cultures were made up of specimens taken from

mixed populations in the field in which the insects had every opportunity of interbreeding with other species. These observations suggest that the species discussed in the present work are reproductively isolated.

It has been shown above that each of the British species is morphologically distinct in the form of the colour pattern and that in some instances this diagnosis can be supported by other morphological characters; the cuticular pattern on the egg chorion is specifically distinct.

The experiments on the effect of two physical factors showed that physiological differences exist between the species. Table I shows that *E. nivalis* and *E. corticalis* are the most resistant to desiccation, that *E. albocincta* and *E. multifasciata* are a little less so, that *E. intermedia* is more dependent on moist conditions, and that *E. nicoleti* is the most susceptible to desiccation. This can be related to the ecological distribution of each species. *E. nicoleti*, the least resistant to desiccation, is restricted to grassland where the humidity is high. *E. intermedia*, a more resistant species, is found on and under moist dead vegetation, *E. multifasciata* is taken on dry litter and the soil surface and *E. albocincta* is taken on and under bark that is normally moist. *E. corticalis* and *E. nivalis*, the most resistant species to dessication, are taken in drier habitats, the former under *Acer pseudoplatanus* bark, which is often very dry, and the latter on dead *Ulex* branches.

The rate of recovery from dosage with carbon dioxide might be expected to be proportional to the surface area/mass ratio of the species and, since the above ratio is high for Collembola, the mean recovery time would be inversely proportional to the mass of the species. It was found that this was so in the experiments (fig. 58 and Table II), and the carbon dioxide anaesthetisation experiments therefore give an indication of the relative sizes of the species, in terms of mass. This size indication is useful as it is difficult to take accurate comparative linear measurements because of distortion by fixing and mounting.

The three species, *E. multifasciata*, *E. nivalis* and *E. intermedia*, appear to be very closely related both biologically and morphologically. These species are similar to the "sibling species" of Mayr (1942), species which differ only slightly morphologically. The use of biological differences may therefore be of importance in assessing the specific status of the species.

X. Summary

1. Systematic criteria at present in use are evaluated and most of them found to be of little use.

2. A new key to nine British species is given.

3. Diagnostic characters of the nine British species are given together with notes on synonymy and the distribution of each species.

4. A new diagnostic character, the sculpture of the egg chorion, is described.

5. Juvenile characters are listed, including one, the trochanteral organ, which is diagnostic of the instar.

6. A key to the juvenile instars is given.

7. The differential effect of two physical factors on closely related species is demonstrated and their significance is discussed.

XI. Acknowledgments

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